1939

The external morphology of the tomato worm (Protoparce sexta Johan.; Lepidoptera: Sphingidae).

Archie Hugh Madden
University of Massachusetts Amherst

THE EXTERNAL MORPHOLOGY OF THE TOMATO WORM

(Protoparce Sexta Johan.; Lepidoptera; Sphingidae)

MADDEN - 1939

THE EXTERNAL MORPHOLOGY OF THE TOMATO WORM

(*Protoparce sexta* Johan.; Lepidoptera; Sphingidae)

by

Archie H. Madden

Thesis submitted for the degree of Master of Science

Massachusetts State College

Amherst, Massachusetts

1939

C O N T E N T S

ACKNOWLEDGMENTS

The preparation of this paper was undertaken under the direction of Dr. G. C. Crampton, to whom the writer wishes to express sincere appreciation for his valuable suggestions and assistance in making up the plates, and his helpful criticism of the manuscript.

To Dr. C. P. Alexander, the writer is indebted for his kind interest, and his criticism of the manuscript; and to Mr. Carl Heinrich and Mr. J. F. Gates Clarke, of the Division of Insect Identification, Bureau of Entomology and Plant Quarantine, for their invaluable assistance in the determination of the synonomy.

INTRODUCTION

The lepidopterous family Sphingidae is characterized by the stout, spindle-shaped body and strong, narrow wings of the adult; the oblique, lateral markings and caudal horn of the larva; and the long tongue case of the pupa. The adults are known as humming-bird moths, hawk moths, or sphinx moths, and certain species are destructive pests in the larval stage.

A considerable amount of attention has been devoted by previous workers to various phases of the external morphology of this family. However, a complete treatment of the morphology of any particular species never has been attempted. One of the purposes of this thesis is to present a detailed study of the external morphology of a typical species, which may serve as an example of the structure of the family.

The tomato worm, Protoparce sexta Johan., was selected for this study because it may be considered a fairly typical species. Then, too, a morphological study of this insect appeared desirable as a supplement to intensive work on its biology, which has been conducted by the writer during the past three years at Quincy, Florida.

P. sexta is one of the largest of the hawk moths, and although restricted to the western hemisphere, its range extends from Canada to southern Brazil, and includes the West Indies and Bermuda. The larvae are among the most destructive of our economic pests. They feed on various wild and cultivated

plants of the family Solanaceae - tobacco, tomato, eggplant, pepper, and potato being the preferred hosts.

Rothschild and Jordan (1903) recognize four distinct geographical races: P. sexta jamaicensis Butler, from the West Indies; P. sexta sexta Johan., from Canada to Honduras westward to the Pacific; P. sexta barbus Cramer, from Costa Rica to Argentina; and P. sexta caestri Blanchard, from Chile. These races appear to exist merely because of differences due to locality, and these differences mainly consist of slight variations in color and markings. Therefore, it is hoped that this study will serve also as a basis for future work on the determination of the validity of these races from the standpoint of comparative morphology.

TAXONOMY

Generic Name

The genus Sphinx was erected by Linnæus (Systema Naturae, Edition X) in 1758. Under this genus were included all of the then known forms belonging to the present families Sphingidae, Ageriidae, and Pyromorphidae. In 1819, Hübner, in his "Verzeichnis bekannter Schmetlinge" (sic!) erected the genus Phlegethontius as one of the divisions of the Linnæan genus Sphinx. The genus Cocytius was created by Hübner at the same time. Under the genus Cocytius were included jatrophæ F., rustica F., and florestan Cramer; while under Phlegethontius were included cluentius Cramer, lucetius Cramer, hannibal Cramer, carolina L., and paphus Cramer. Each of the above genera was a mixture of two genera; jatrophæ (a synonym of antæus Drury), and cluentius forming one genus; and rustica florestan, lucetius, hannibal, carolina, and paphus the other. It was not until 1856 that Burmeister, in his "Sphingidae Brasiliens" (Abhandlungen naturforschenden Gesellschaft zu Halle, Vierteljahrsbericht, p. 62), erected the genus Protoparce for the type species rustica, which he redescribed. Thus from the standpoint of priority, Protoparce should give way to Phlegethontius. However, Rothschild and Jordan (l.c.) cite antæus as the genotype of Cocytius, and cluentius as

the genotype of Phlegethontius. Since cluentius and antæus are congeneric, as shown above, Phlegethontius therefore falls under the synonomy of Cocytius. A summary of the synonomy of Protoparce is presented below:

NAME	GENOTYPE	DATE
Sphinx Linnæus	(partim; ocellata)	1758
Manduca obscura Hübner		1806
Cocytius Hübner	(partim; antæus)	1819
Phlegethontius Hübner	(partim; cluentius)	1819
Protoparce Burmeister	rustica	1856
Macroglilia Walker ...	(partim; includes rustica)	1856
Diludia G. & R.	brontes	1865
Syzygia G. & R.	afflicta	1865

Specific Name

The species was first described by Boas Johansson as *Sphinx sexta* in a doctor's thesis (Centuria Insectorum Rariorum, p. 27) presented before the medical faculty of the Royal Academy, Upsala, and published in 1763. The following year (1764) the species was redescribed by Linnæus (Mus. Ludov. Ulricae, p. 346) as *Sphinx carolina*. Since that date the species has been redescribed a number of times by various workers. A summary of the synonomy is as follows:

carolina	Linnæus	1764
carolinus (!)	Emmons	1854
nicotianæ	Ménétriés	1857
lycopersici	Boisduval	1875
quinquemaculata	Mann	1877

EXTERNAL MORPHOLOGY

General Description

P. sexta is a moderately large moth with an alar expansion from three to five inches. The general color of the dorsal surface of the body and fore-wings is dark brownish-grey. The thorax is marked by several white spots, which are ringed with black. The fore-wings have a somewhat variegated appearance, owing to the presence of a number of wavy, dark-brown, transverse bands. There is a broad spot at the base of the fore-wing, and a smaller white spot at the end of the discal cell. The outer margin bears a short, dark-brown fringe, in which several white spots occur. The hind wings are darker than the fore-wings, and are traversed by a number of broken, oblique cross-bands. A short whitish fringe occurs on the outer margin of the hind wing. This fringe is spotted with brown.

Two lateral, black spots are borne on the dorsal surface of the base of the abdomen, and six pairs of orange spots occur on the six succeeding segments. These spots become progressively smaller toward the tip of the abdomen, and each pair is associated with a pair of median, white spots. The number of orange spots is not always constant, and occasional specimens may exhibit five pairs instead of the normal number of six.

The ventral surface of the wings is light brownish-grey, and is crossed by a few bands of a darker brown color. The

ventral surface of the body is grey with three or four median, dark-brown spots on the abdomen. The palpi and the ventral surface of the thorax are heavily clothed with long hairs.

The males, although usually slightly smaller in size, are similar in appearance to the females. However, the antennae in the male are much larger and more complex in structure than those of the female.

Head

Head Capsule (Figs. 1, 4, 6)

The head capsule is a comparatively simple structure exhibiting a limited number of sclerites. Viewed from the dorsofrontal aspect, its general shape is approximately oval. However, since it is slightly flattened posteriorly, and as the mouthparts project beyond the anterior margin, there is an approach toward a triangular outline. The shape of the head capsule is practically identical in both sexes.

The most prominent sclerite of the anterior region of the head capsule is the fronto-clypeus (fc). This is a broad, slightly convex sclerite, demarked laterally by the ocular sutures (os) which extend from the antennal sockets ventrally to the subgenal sutures. Dorsally, slightly arched frontal sutures (fr) extending between the antennal sockets separate the fronto-clypeus from the vertex. The ventral portion of the fronto-clypeus is abruptly convex, forming a blunt, snout-like

protuberance which projects forward and downward over the bases of the mouthparts.

The subgenal sutures (sgs) separate the fronto-clypeus from the subgenal region, which apparently merges on either side of the head with the triangular-shaped lobes representing the rudimentary mandibles. The subgenal sutures are arched above the frontal pits (fp), which are clearly discernable as vertically elongated depressions marking the invaginations forming the anterior tentorial arms. Since these pits occur only on the epistomal or subgenal sutures, they form a means of determining the point of division between the frons and the clypeus. Therefore, that portion of the fronto-clypeal sclerite below or anterior to the frontal pits might possibly be considered as being the clypeus. However, the principal dilator muscles of the cibarium rise upon the area above and behind this point (Fig. 6, dclb), and Snodgrass (1935) states that these muscles arise on the clypeus. Therefore, according to this conception, the clypeus forms a large part of the frontal region of the head, and the frontal pits arise on the subgenal sutures.

The compound eyes (e) are dark brown, subglobular, and prominent. They extend over about two-thirds of the head, and from the frontal aspect compose nearly the entire lateral margins. Their greatest development, however, is ventroposteriorly and they project considerably below and behind the posterior and ventral regions of the head. The inner margins are curved slightly, and are approximated ventrally to a

considerable degree. The eyes are separated from the frontoclypeus by narrow ocular sclerites (oc) which apparently terminate dorsally at the antennal sockets. Ventrally these sclerites appear to merge with the subgenal regions of the head. The development of the eyes has completely obliterated the genae.

The antennae (ant) are located laterally and almost adjacent to the inner margins of the compound eyes. Antennal sutures (as), which touch the inner margins of the eyes laterally, demark the narrow antennal sclerites (asc) which border the antennal sockets. The antennal sclerites are expanded to a considerable extent laterally, and each of these broader areas is produced into a blunt protuberance which extends into the antennal socket. These protuberances, which are termed the antennifers (anf), form the articulatory points for the basal segments of the antennae.

The vertex (vx) is a large, convex area forming the top of the head. The dorsal edge of the frontal sutures is projected upward slightly into the vertex at the center, suggesting a vestigial coronal suture, which in more generalized insects divides the vertex (laterally) into two parietal sclerites. Traces of the extent of the coronal suture are still further indicated by a pale, lightly-sclerotized line extending medially to the top of the head. The two lateral ocelli, which are located on the vertex in certain Lepidoptera, are absent in gexta. The vertex is limited posteriorly by the postoccipital suture (pos) which separates it from the

postocciput. The occiput (ocp) is not separated from the vertex by a distinct suture, but it may be identified with the posterior portion of the epicranium.

The postoccipital sclerite (poc) occurs mainly as a narrow sclerite which borders the occipital foramen dorsally and laterally. Dorsally, it widens into a semicircular lobe or flap which projects outward, roof-like, over the occipital foramen. Internally, the postoccipital suture forms a prominent postoccipital ridge (por) to which are attached the anterior ends of the muscles which move the head. The postocciput is enlarged ventrally into two lobe-like expansions, the occipital condyles (ocd), which serve as articulatory points for the lateral cervical sclerites. Mesally the occipital condyles fuse with the postoccipital ridge and the posterior arms of the tentorium (pt), so that the latter appear to arise from the postocciput.

The occipital foramen (ocf), or opening from the head to the neck through which the alimentary tract and nervous system enter the body, occupies a considerable portion of the posterior region of the head. The posterior arms of the tentorium form a bridge across the lower part of the foramen, between the occipital condyles. The ventral margin of the foramen is formed by the hypostomal bridge (hbr).

The postgenae (pge) are the most conspicuous sclerites of the posterior part of the head. These sclerites occupy the spaces between the postocciput and the compound eyes, and are separated from the postocciput by the postgenal sutures (pgs).

They extend anteriorly to the ventral surface of the head where they merge into the subgenal region. They are quite broad posteriorly, but taper abruptly toward the subgenal area.

The tentorium is composed of two pairs of chitinous invaginations of the ectoderm. The first pair, or anterior arms (at), arise on the subgenal sutures near the margin of the labrum, their external manifestations being the frontal pits. The anterior arms extend backward through the interior of the head capsule, connecting with the second pair of invaginations, or posterior arms, slightly mesad of the occipital condyles. The gular pits, which constitute the external manifestations of the posterior arms, are not apparent in sexta. However, from the interior of the head, it may be seen that the posterior arms arise close to the lateral margins of the occipital condyles. The tentorium functions as an internal support for the head capsule, and as a structure for muscle attachment.

Antennae (Figs. 2, 3, 5)

The antennae of the male are stout and slightly pectinate, while those of the female are more slender and thread-like. The number of segments varies from about 72 to 76 in both sexes.

The basal segment, or scape (scp), which articulates with the antennifer, is subcylindrical and considerably larger than the succeeding segments. The second segment, or pedicel

(p), is much smaller and is somewhat bulbous. In the female antennae, the majority of the remaining segments, which constitute the flagellum (fl), are cylindrical and of approximately the same size. However, the more distal segments become progressively smaller toward the tip. The tip in both sexes is composed of several relatively small segments arranged in the form of a recurved hook.

In the male, each segment beyond the pedicel is broadly rounded at the dorsal margin and is rather distinctly dilated laterally so that these segments are somewhat triangular in cross-section. Each segment beyond the pedicel, excepting several of the distal segments of the tip, bears a subapical and a subbasal vertical row of long cilia (cil). These two rows of cilia become fused dorso-laterally, forming a flattened semicircle from the lateral aspect of the segment (Fig. 3).

The dorsal margin of the antenna in both sexes is thickly clothed with long, flattened, overlapping scales. Each segment of the flagellum, with the exception of the first five and the distal segment of the tip, bears a tooth-like projection, or sense cone (scn), ventrally near the apex of the segment.

Mouthparts (Figs. 1, 4, 6)

The labrum (lm), or upper lip, consists of a narrow, transverse sclerite which is partly concealed from the cephalic aspect by the bulbous margin of the fronto-clypeus. The labrum is produced into a mesal and two lateral lobes. The mesal

lobe, which represents the epipharnyx (ep), in part, is relatively small; but the two lateral lobes, or pilifers (pfr), are large and prominent and their inner margins bear a number of setae. The pilifers resemble mandibles superficially, but a closer examination shows that the mandibular lobes are distinct.

The mandibles (md) are rather large, convex, triangular lobes lying behind the pilifers. Although rather conspicuous, they are rudimentary and there is no point of articulation with the head capsule. The mandibles arise from the subgena, from which they are not clearly demarked by definite sutures, although vestiges of such sutures may be detected in some specimens.

The maxillae are the largest and most important of the mouthparts. The cardo (cd), or basal segment, is triangular-shaped and it articulates with the anterior margin of the sclerotized portion of the labium. The stipes (stp) is curved medally and is subcylindrical in cross-section. The stipes is almost completely concealed beneath the projecting portion of the subgena. The single-segmented maxillary palpus (mp) is somewhat palmate, and is greatly reduced in size. It is borne on the anterior portion of the stipes near the point of attachment to the galea. The palpus is clothed with stiff bristles, and long, whitish, hair-like scales.

The galeae (ga) constitute the greater part of the maxillae, forming the prominent tongue or proboscis. The inner surfaces of the galeae are concave, and the inner

margins are held together firmly by interlocking grooves and spines to form a long sucking tube. The basal portion of the tube opens into the sucking pump (spm) by which liquids are drawn up the tube and forced backward into the stomach. The sucking pump is well developed, and narrows posteriorly into the oesophagus (oes). The floor of the pump is formed by the hypopharnyx (hy), which lies just above the salivary duct.

When not in use, the proboscis is held tightly coiled beneath the head. The extended proboscis is approximately twice the length of the body, and the average length is about 7⅘ mm. According to Schmitt (1938), extension of the proboscis is effected by the compression of the cylindrical stipites which forces the blood out into the galeae causing them to straighten. Muscles within the galeae cause them to recoil when the tension on the stipites is relaxed.

The sclerotized portions of the labium are limited to a small area around each labial palpus, and a short, narrow median strip proximad of the base of the proboscis. The remainder of the labium probably is represented by the membranous portion of the ventral surface of the head. The labium is supported posteriorly by a narrow hypostomal bridge.

The most prominent portion of the labium consists of the three-segmented labial palpi (lp). The first, or basal segment, of the labial palpus is large and well developed. This segment is curved forward and upward in such a way that the remaining segments are applied closely to the anterior

part of the head. The second segment is also large and stout, but the third segment is relatively minute. The third segment is oval in shape, and bears a ventral depression, or pit, at the distal end. This pit is lined with short hairs, and it probably represents a sensory organ. The labial palpi are heavily clothed with long hairs, and the proboscis is almost completely concealed by them when it is coiled beneath the head.

Thorax

The thorax is typical of the order, in that the mesothorax has been greatly developed at the expense of the pro- and metathoraces. The prothorax is small and largely membranous, while the metathorax, although heavily sclerotized, is much reduced in size as compared with the mesothorax. The meso- and metathoraces are united closely, forming a distinct wing-bearing region, which Snodgrass (l.c.) calls the pterothorax.

Cervix (Figs. 13, 16)

Although treated herein under the thorax, the cervix or neck is an intersegmental region which lies between the head and the prothorax. It is almost entirely membranous, sclerotization being limited mainly to a pair of V-shaped lateral cervical sclerites (lc) located at the sides of the neck.

The apex of the V articulates with the anterior margin of the prothoracic episternum, and is prolonged beyond the point of articulation as a short, free stem extending caudad of the margin of the episternum. The distal ends of the anterior arms, or cephaligers (cg), articulate with the occipital condyles, while the ends of the ventral arms are united by an extremely narrow, transverse bridge. Crampton (1926) calls attention to the possibility that this sclerite may be homologous with the presternite, or intersternite. Thus it may be called the presternum (pm). The presternum fuses mesally with the anterior margin of the precoxale (pr).

The flexibility of the cervix, and the articulations of the lateral cervical sclerites permit free movement of the head in any direction.

Prothorax (Figs. 8, 13, 18)

The prothorax, or anterior segment of the thorax, lies directly caudad of the neck region. It is greatly reduced in size, and similarly to the cervix, it is largely membranous. The anterior pair of legs are borne on this segment.

The pronotum (pn) consists of three small plates partially fused together and arranged in the form of a Y. The posterior plate bears two short, lateral projections near the distal end. Behind these projections, it tapers toward the base, which is slightly enlarged. The base or proximal portion articulates with the anterior margin of the mesothoracic

prescutum, which is withdrawn into a bowl-shaped depression at this point. The larger, anterior arms of the Y are curved outward and downward around the dorsal portion of the anterior opening into the thorax. The posterior margins of these plates are broadly rounded, and their ventral margins are partially fused with the episternal sclerites. Two fleshy, somewhat flattened lobes called the <u>patagia</u> (pg) are borne on the dorsal margins. Directly behind the patagia lie another pair of fleshy lobes, called the <u>parapatagia</u> (par), by Schultz (1914). This pair is somewhat larger than the patagia, and they extend downward on either side into the pleural region of the prothorax.

The <u>episternum</u> (eps_1) is a convex sclerite partially fused with the ventral margin of the pronotum. The posterior margin is broadly rounded, and the <u>pleural suture</u> (ps), which normally separates the episternum from the posterior epimeron, is very distinct. However, all traces of the epimeron have disappeared. The pleural suture forms a prominent internal ridge for muscle attachment. This ridge is produced ventrally on either side into two <u>pleural arms</u> (pa), which fuse with the <u>furcal arms</u> (fa).

A small, triangular <u>trochantin</u> (trn) is associated with the ventral margin of the episternum. The trochantin articulates with the <u>coxa</u> (cx) of the prothoracic leg. The episternum is connected with the anterior portion of the sternum by a very narrow precoxal bridge, or <u>precoxale</u> (pr), which passes in front of the coxal cavity. The postcoxal bridge, or

postcoxale, which frequently connects the epimeron with the sternum behind the coxal cavity, is absent.

The basisternum (bs_1), or anterior portion of the sternum, is reduced to a narrow region representing the edges of a deep median fold, which forms an internal plate, or ridge. The basisternum broadens slightly into a posterior furcasternum (fs_1), which may be distinguished by a deep, pit-like depression. This depression marks the invagination giving rise to the internal apophyses, or furcae, which are produced dorsally as the furcal arms. The furcasternum connects with the narrow, anterior portion of the spinasternum (ss). The spinasternum extends almost vertically inward, and then outward, forking posteriorly into two broad, lateral arms. The upward extension of the spinasternum forms a strap-like process. The lateral arms are approximated to the anterior margin of the mesothoracic basisternum, but are not fused with it.

Mesothorax (Figs. 8, 13, 18)

Notum

The anterior mesothoracic tergite, or prescutum (psc), is a small, strongly convex sclerite, which lies partially in a deep, semicircular cleft in the anterior margin of the scutum. it is directed ventrad, and is almost invisible from the dorsal aspect. A broad bowl-shaped hollow or depression occurs near the anterior margin; and the base of the pronotum,

which articulates with this margin, is partially withdrawn into the hollow. The lateral margins are produced into two narrow, plate-like processes, or prealars (pra), which extend to the pleuron on either side.

The scutum (sct_2), which is the next sclerite in order, is the largest of the thoracic tergites. It is widest at the base, and is about as broad as long. The anterior margin is deeply cleft and the median carina, which is quite distinct posteriorly, becomes obliterated as it passes forward. Directly caudad of the prealar sclerite, the lateral margin is deeply notched to form the tegular incision (ti). Back of this point, the lateral margin forms a flat projection known as the anterior notal wing process, or suralare (sur), which serves as an anterior pivotal point for the wing. The anterior margin of the suralare is straight, while the posterior margin is strongly recurved.

In the membrane, laterad of the tegular incision and the suralare, lie two plates which compose the subtegula (st). The anterior plate is directed mesad into the tegular incision, while the longer, rod-like, posterior plate passes backward to the pleural wing process, and serves as a prop for the anterior plate.

The tegula (teg) is an extremely large, thin plate which is rather strongly convex anteriorly. The broadly rounded anterior margin is slightly cephalad of the tegular incision, while the narrower posterior portion extends backward nearly to the base of the scutum. The antero-lateral

margin is produced backward into a long slender process, which passes beneath the base of the fore-wing. The tegula is supported by the subtegula, to which it is attached ventrally.

The postero-lateral margin of the scutum is produced into a flat extension containing two lobes, with a deep notch lying between them. The anterior lobe, which represents the posterior notal wing process, or adanale (ad), is long, slender, and finger-like. It serves as the posterior articulatory point for the wing. The posterior lobe is shorter and stouter, and is called the postadanale (pad).

Between the suralare and the adanale, the lateral margin of the scutum is extended into a forward projecting process, called the adnotale (al). The adnotale also functions as an articulatory point for the wing. A deep emargination in the edge of the scutum lies between the adnotale and the posterior margin of the suralare. This is called the notal incision (ni).

The scutellum (scl_2) is a smaller, V-shaped tergite, caudad of the scutum, with which it is closely associated. The membranous axillary cords (axc) are continuous with the posterior marginal fold of the scutellum, and they extend along the posterior margins of the postadanales to the anal regions of the wings.

The postscutellum ($pscl_2$) is a very narrow, transverse sclerite, lying partially concealed within a depression between the scutellum and the scutum of the metathorax. The intersegmental fold between the postscutellum and the

metathoracic scutum gives rise to a huge internal postphragma (ph), which is developed to such an extent that the dorsal vessel and alimentary tract are forced into the ventral region of the body cavity in order to pass beneath it. The postphragma affords one of the chief points of attachment for the dorso-lateral mesothoracic muscles.

Pleuron

The pleuron of the mesothorax is divided by a vertical pleural suture (ps), extending from the pleural wing process to the coxa, into an anterior episternum and a posterior epimeron (em_2). A transverse anepisternal suture (a), which extends diagonally across the episternum almost to the pleural suture, divides the episternum into a dorsal anepisternum (aes), and a ventral katepisternum (kes). A lobe-like sclerite, or preepisternum (pes), which is fused ventrally with the basisternum, is separated from the anterior portion of the katepisternum by the preepisternal suture (u). The katepisternum is continued ventrally as a narrow precoxale, which fuses with the furcasternum.

The dorsal margin of the anepisternum is strongly folded, and this fold may represent the basal portion of the basalare (ba). The basalare proper is a small, partially detached, triangular plate, just dorsad of the fold, upon which important wing muscles are inserted.

The epimeron is almost V-shaped, owing to a deep incision in its dorsal margin. A distinct suture cuts off the

anterior portion into a subcircular region, or fold, which Shepard (1930) calls the preepimeron (pem). The anterior margin of the preepimeron overlies the pleural suture, and its upper portion lies in a cavity parallel with the suture. This cavity extends forward into the anepisternum. The narrow antero-dorsal portion of the epimeron is strongly convex and overlies the cavity so that it almost touches the convex posterior margin of the anepisternum. It is produced dorsally into a pleural wing process (wp). The posterior arm of the subtegula passes beneath the basalare to fuse with the anterior portion of this process. The basalare lies just cephalad of the pleural wing process, to which it is partially attached.

Behind the wing process, in the membrane above the epimeron, lies the posterior epipleurite, or subalare (sa). Important wing muscles are inserted upon this plate also, and it is invaginated medially for this purpose. Directly behind the subalare is a small, narrow plate which apparently represents a second subalare.

The upper posterior margin of the epimeron bears a deep, semicircular emargination for the accomodation of the anterior portion of the metathoracic spiracle. The epimeron is not produced ventrally to form a postcoxale, but tapers to a sharp point immediately caudad of the meron. The furcal arms fuse internally with the posterior portions of the epimera.

The coxal region of the leg is attached to the ventral margins of the episternum and epimeron. A basicostal suture (bc) divides the coxa into an anterior eucoxa (ecx_2), and a

posterior meron (me_2). The meron represents the distal extension of the postarticulatory region of the basicoxite, which has become greatly developed in this direction. A triangular plate, lying at the base of the coxa between the lower edge of the katepisternum and the meron, is separated from the eucoxa by the basicostal suture. Snodgrass (1909) calls this sclerite the trochantin, but Shepard (l.c.) calls it the epicoxal piece (x) and states that it undoubtedly represents the exposed part of the basicoxite anterior to the pleural articulation of the coxa.

The mesothoracic spiracle (sp) has migrated forward, and lies in the pleural membrane of the prothorax caudad of the pleural extension of the parapetagia.

sternum

The basisternum (bs_2) of the mesothorax is a broad, wedge-shaped sclerite. It is inrolled to form a mid-ventral suture (mv) which gives rise to an internal, keel-shaped ridge.

The furcasternum (fs_2) is a small, triangular, deeply infolded plate which is fused with the katepisternum. The median invagination gives rise to a pair of broad furcal arms which are directed slightly caudad. The ends of these arms fuse with the posterior portions of the epimera in such a way as to form a brace across the caudal end of the mesothoracic cavity. There is no apparent connection between the furcal arms and the pleural ridge, which is a very unusual condition in insects. However, the structure of the endoskeleton is so

complicated by additional invaginations and infoldings that this point could not be determined definitely.

Metathorax (Figs. 8, 13)

Notum

The scutum (sct_3) of the greatly reduced metanotum consists of two lateral, lobe-like sclerites. The anterior margins are produced slightly, forming the anterior notal wing processes, or suralares (sur). The flattened posterior margins are produced into two long, narrow projections which represent the posterior notal wing processes, or adanales (ad). The scutellum (scl_3) is a narrow, transverse plate lying across the base of the scutum. The anterior margin is sinuate, and the lateral margins are produced into membranous axillary cords (axc) which extend to the anal region of the hind wings. The postscutellum ($pscl_3$) is an extremely narrow sclerite caudad of the scutellum. It is mainly represented by a deep invagination which gives rise to a large internal phragma upon which a great number of muscles are attached. The membranous portion of the first abdominal tergite is attached to the posterior margin of the postscutellum.

Pleuron

The metapleuron is divided by a vertical pleural suture (ps) into an anterior episternum (eps_3) and a posterior epimeron (em_3). The episternum fuses ventrally with the basisternum, and on its dorsal margin there occurs a weakly

sclerotized, subcircular pad. Shepard (l.c.) calls this structure the anterior basalare, or basalar pad (bp). The metathoracic spiracle (sp) lies almost directly beneath this pad and is partially concealed by it. The basalare (ba) consists of a small, quadrate plate which lies immediately above the basalar pad. The pleural wing process (wp) is a small, vertical plate caudad of the basalare. The wing process, bacalare, and basalar pad represent structures for wing support and for attachment of the wing muscles.

The dorsal margin of the epimeron is deeply emarginated, and in the membrane above this emargination lies the posterior epipleurite, or subalare (sa). A latero-ventral extension of the postscutellum fuses with the posterior region of the epimeron to form a postalar bridge. The upper portion of the postalar bridge becomes deeply infolded and merges with the invagination of the postscutellum. Directly below the point of fusion, the fold thus formed widens into a posterior pocket. A deeply folded plate bearing a tergo-pleural groove passes forward from the first abdominal tergite and fuses with the posterior margin of this pocket, and thus forms a strong point of attachment between the thorax and abdomen.

The coxa is closely attached to the pleuron and consists of an anterior eucoxa (ecx_3) and a posterior meron (me_3). A triangular epicoxal piece (x) lies between the eucoxa and the ventral margin of the pleuron, as in the mesothorax.

Sternum

The metathoracic basisternum (bs_3) is reduced to a very narrow, transverse plate which fuses with a narrow ventral extension of the episternum. This extension of the episternum forms a narrow precoxale in front of the coxal cavity. The furcasternum is correspondingly reduced, and the apophyses arising from it branch dorsally into an anterior and a posterior pair of furcal arms (fa). The anterior arms are short and stout, while the posterior arms are much longer and fuse with the ventral margin of the epimeron, forming a narrow precoxale. The membrane of the anterior margin of the basal abdominal sternite is attached to the posterior margin of the precoxale. There is no apparent connection between the furcal arms and the pleural ridge. This is similar to the condition existing in the mesothorax.

Legs (Figs. 7, 11, 12)

Coxae

The coxa (cx) of the prothoracic leg is an elongated, cylindrical segment which is broadest near the base and tapers considerably toward the distal end. It articulates proximally with the trochantin, which is closely associated with the ventral margin of the episternum.

The coxae of the meso- and metathoracic legs are immovably united with the pleura. They are separated by a meral suture, or basicostal suture (bc), into an anterior eucoxa (ecx) and a posterior meron (me). The eucoxa and meron are

produced distally into trochantifers which articulate freely with the condyles of the trochanter.

Trochanters

The trochanters (tr) of all the legs are subglobose and of about equal size. The condyles of the trochanter articulate with the trochantifers of the coxa. There is no distal point of articulation, as the trochanter is immovably attached to the femur at this point.

Femora

The femora (fe) of the prothoracic and mesothoracic legs are nearly twice the length of those of the metathoracic legs. The posterior margin of the femur of the prothoracic leg is broadly rounded proximally but tapers sharply toward the distal end, thus providing a space for the accommodation of the epiphysis when the femur and tibia are folded together. The femora are clothed with long hairs, but do not bear spines, spurs, or setae.

Tibiae

The tibia (tb) of the prothoracic leg is rather short and stout and carries a prominent, claw-like epiphysis (epi), which bears a row of fine bristles on its inner margin. The base of the epiphysis rests in a long cavity in the posterior margin of the tibia.

The tibia of the mesothoracic leg is about one and one-half times the length of the prothoracic tibia. It is rather

slender throughout the greater part of its length, but widens perceptibly toward the distal end, which bears a pair of stout spurs (spu). The outer spur is about twice the length of the inner spur, and is nearly one-half the length of the tibia. The tibia of the metathoracic leg is about twice the length of the prothoracic tibia, and is armed with two pairs of long spurs (spu). The proximal pair of spurs articulates with the posterior or inner margin of the tibia, toward the distal end, while the distal pair articulates with the distal end. The outer spur of each pair is the longer.

Tarsi

The tarsus is composed of five segments. The basal segment, or basitarsus (bt), is the longest, and it is longer in the middle and hind legs than in the fore-legs. In the middle, or mesothoracic, leg it is over three times as long as any of the remaining segments. The tarsal segments become progressively shorter, and the shortest, or distal segment, is known as the distitarsus (dt).

The posterior margin of the fore-tarsus bears three irregular rows of stout spines. The anterior margin of the basitarsus bears a number of irregularly placed spines, and four or five medium-sized spurs, the longest being at the distal end of the segment. Each of the tarsi of the middle and hind legs bears four rows of spines. In the proximal portion of the basitarsus, especially in the mid-tarsus, the posterior row of spines is long and bristle-like.

Pretarsus (Fig. 15)

A claw-bearing region, or pretarsus, is borne on the tip of the distitarsus of each leg. The most prominent part of the pretarsus is the two large, curved claws, or ungues (ung), which articulate with the dorsal margin of the distitarsus by means of a small, hook-shaped process called the ungifer. Two membranous pulvilli (pv) arise from the membrane at the base of the claws. The pulvilli are setiform and are covered thinly with short hairs. Proximad of the bases of the claws, lies a broad sclerite with a median elongation at the distal margin. The basal portion of this sclerite apparently represents the planta (pl), while the distal elongation is probably the empodium (emp). The arolium (ar), or median lobe between the claws, has been reduced to a small membranous area which lies above the empodium. On its dorsal surface there arises a tiny, cylindrical, sclerotized process, or orbicula (or), which bears a single seta on its distal end. The base of the planta is separated slightly from a narrow, ventral, sclerotized area, or unguitractor (ut), which is partially withdrawn into the distitarsus. The unguitractor tendon (utt) is attached to the proximal margin of the unguitractor and extends upward into the tibia.

Wings

The wings are large and powerful and their shape is quite typical of the family. Media has been reduced to a three-branched condition, and there is a reduction in radius in the hind wing. This condition is characteristic of the sub-order Frenatae. The venation is interpreted in the following discussion according to the Comstock-Needham system.

Fore-wings (Fig. 9)

The fore-wings, or primaries, are elongate-triangular in shape, and their length is about two and one-half times their breadth. The apical angle is acute, and the anal angle is distinct. The outer margin is crenulate and is somewhat shorter than the inner margin, which is slightly sinuate.

The costa (C) is marginal, and the subcosta (Sc) is entire and reaches the margin about two-thirds the distance from the base to the apex. Radius is five-branched, and R_1 rises proximad of the upper angle of the discal cell (dc). The stem of R_2 and R_3 rises closer to the upper angle, while the stem of R_4 and R_5 rises at the upper angle. The basal portion of media has atrophied (hypothetical position indicated by dotted lines), therefore the three branches of media appear to rise from the end of the discal cell. M_1 rises from the upper angle at the same point as the stem of R_4 and R_5; M_2 rises about half way across the end of the cell; while M_3 rises from the lower angle.

Cubitus is two-branched. The first branch (Cu_1) rises slightly proximad of the lower angle of the discal cell, and is separated from M_3 by a short medio-cubital cross-vein (m-cu). The second branch (Cu_2) rises from the lower portion of the discal cell about half the distance to the base of the wing. The first anal has atrophied but a vestige of it remains as a distinct anal furrow (indicated by a dotted line). The second anal (2nd A) is retained, but all that remains of the third anal is a basal portion which appears as a basal fork of the second anal. The distal portion of the third anal is coalescent with the distal portion of the second anal.

Hind wings (Fig. 10)

The hind wings, or secondaries, are much shorter and wider than the fore-wings. They are more triangular in shape, and the apical and anal angles are broadly rounded. A distinctive feature of the venation of the hind wings, which is also typical of the family, is the prominence of the basal portion of R_1. This free part of R_1 has the appearance of a cross-vein, and is fully as stout as the other veins. In the few cases in which this condition exists in other families of Lepidoptera, the free portion of R_1 is rarely as strong as the other veins. The remainder of R_1 is coalescent with the subcosta and reaches the margin as $Sc+R_1$. The four branches of the radial sector have coalesced to form a single vein (Rs). The three branches of media, and the two branches of cubitus arise from the discal cell in the same manner as in the

fore-wings. The first anal has atrophied, but the second and third anals have been retained.

A frenulum (f) is borne at the humeral angle of the hind wing. In the male, the frenulum consists of a stout, spine-like organ which projects beneath the fore-wing. The end is received in a flat, chitinous catch, or frenulum hook, which rises from the membrane between the costa and the subcosta on the ventral side of the fore-wing. In the female, the frenulum consists of a group of about ten spine-like bristles. The tips of these bristles may be engaged in a cluster of hairs, called the retinaculum, which occurs ventrally at the base of cubitus, in the fore-wing. The purpose of the frenulum is to coordinate the movement of the wings in flight.

Axillary sclerites (Fig. 8)

The fore-wings are attached to the body by an articular membrane which extends from the tegula caudad to the axillary cord. This membrane contains several sclerites which act as articulatory points between the wing veins and the notal wing processes.

At the anterior margin of the wing base, there is a subquadrate plate, the parategula, or humeral plate (hp), which articulates with the base of the costal vein. In the articular membrane, caudad of the humeral plate, lies an irregularly shaped sclerite known as the notale, or first axillary (lax). The anterior arm of this sclerite articulates with the lateral margin of the suralare (sur) and the head of the subcosta (sc),

which is an extension of the subcostal vein. The posterior portion of the first axillary articulates with the adnotale (al), while the antero-lateral portion articulates with the mediale, or second axillary (2ax). The second axillary is a narrow sclerite which lies parallel to the lateral margin of the first axillary. It articulates anteriorly with the base of the radial vein, and ventrally with the pleural wing process. The basanale, or third axillary (3ax), is a triangular sclerite caudad of the second axillary. The flexor muscle of the wing is inserted on this sclerite. It articulates anteriorly with the posterior end of the second axillary, and is associated posteriorly with the base of the anal vein. A very small, narrow sclerite, or fourth axillary (4ax), lies between and articulates with the third axillary and the adanale (ad). A triangular plate, distad of the second and third axillaries, represents the proximal median plate (m). A second median plate (m') lies slightly distad of the first plate. At the base of the anal vein, caudad of the proximal median plate and the third axillary, there occurs a basal knob, or basoplica (bpl). Anterior to the basoplica lies a pocket, or marsupium (r), into which the basoplica fits when the wings are flexed horizontally over the abdomen.

The articulatory membrane of the hind wing extends from the base of the frenulum caudad to the axillary cord. The notale, or first axillary (1ax), is an elongated, irregularly shaped plate, which articulates anteriorly with the head of the subcosta (sc) and laterally with the suralare (sur).

Posteriorly, it articulates with the mediale, or second axillary (2ax), which in turn articulates anteriorly with the base of radius and distally with the median plate and third axillary. The basemale, or third axillary (3ax), articulates anteriorly with the median plate (m) and proximally with a rather elongated adumale (ad). The basoplica (bpl) occurs at the base of the anal vein and the harpurium (r) lies directly anterior to it, as in the fore-wing.

Abdomen

The abdomen (Fig. 14) is elongate-conical, or spindle-shaped, which is typical of the family. It is composed of ten segments, or somites, but the terminal segments are reduced and modified to form the genitalia and are retracted within the last visible segment. Thus there are only eight evident segments in the male, and seven in the female.

The sclerotized portions of the segments consist of a dorsal plate, or tergite (t), and a ventral plate, or sternite (s). The tergites and sternites are separated by a membranous pleural region, which bears the seven abdominal spiracles (sp). The segments are connected by conjunctival membranes, and each tergite and sternite normally overlaps the following tergite and sternite. A narrow, anterior marginal area, or acrotergite (atg), is demarked by a faint antecostal suture (acs) in all the tergites of the unmodified segments, with the exception of the first. This suture demarks the position of an internal

ridge, or antecosta, upon which the principal dorso-longitudinal muscles are attached. The tergites, mentioned above, also bear a double row of stout spines on their posterior margins. A single row of weaker spines occurs on the posterior margins of the corresponding sternites.

The first abdominal tergite is greatly reduced and bears a long, narrow plate on its lateral margin. This plate extends forward and fuses with the edge of the fold in the posterior margin of the metathoracic postscutellum. A deep groove, or fold, occurs in this plate, which according to Forbes (1923) represents the tergo-pleural groove (tp). Below the plate lies a small pleural sclerite (pu). The anterior portion of the second tergite is extended into the pleural region and probably represents the second abdominal pleurite, although it is not demarked from the tergite by a suture. None of the remaining segments has sclerotized areas in the pleural region.

The first abdominal sternite is not distinct, but fuses with the second sternite to form a wide plate lying beneath both the first and second tergites. A deep invagination occurs near the upper, anterior margin of this plate, which gives rise to a hook-shaped process upon which muscles are attached.

The orifice of a scent organ (so) lies in the pleural membrane, above the dorsal margin of the second sternite, in the male. A groove, or fold, extends backward from this opening to a point above the fourth sternite. The orifice is covered with a tuft of long hairs.

Male genitalia (Figs. 14, 17)

Considerable confusion exists with regard to the terminology used in connection with the parts of the male genitalia in Lepidoptera. It, therefore, becomes necessary to adhere to the usage of one particular worker in this field. The terminology of Eyer (1924) has been employed almost exclusively below.

The male genitalia is composed of the highly modified ninth and tenth abdominal segments, which are normally almost completely retracted within the eighth. The dorsal portion, or tergum (tg), apparently represents the ninth tergite. It is strongly arched dorsally and tapers slightly toward its posterior extremity. The tergum fuses ventrally with the ninth sternite, or vinculum (v), which is a narrow sclerotized band, or ring-like plate enclosing the basal portion of the genitalia. The vinculum is produced anteriorly to form a medioventral invagination, or saccus (su).

Articulating with the posterior margins of the vinculum are the paired appendages, or harpes (hr), which function as clasping organs during mating. Each harpe is somewhat spatulate in shape, and, with the exception of certain regions, is very weakly sclerotized. The inner surface is slightly concave and is covered with numerous long hairs. The dorsal region is thickened and rather heavily sclerotized; while the ventral region, or sacculus (sac), is also heavily sclerotized and is produced into a curved inner process, the distal portion

of which is completely separated from the remainder of the harpe. This distal portion consists of a ventral prong, which is separated by a deep incision from a broader dorsal process with a partly serrate dorsal margin. The shape of the sacculus is constant within the species, and is thus of importance in classification.

The inner dorsal angles of the harpes are connected by a sinuate plate, or transtilla (ts). The ends of the transtilla are deeply invaginated to form points of articulation for the harpes. Immediately below the transtilla, lying within the ring-like vinculum, is a cone-shaped membranous tube, or anellus (au), through which the aedeagus enters the abdomen. The anellus is invaginated to form a membranous tube surrounding the aedeagus. Externally, the ventral portion of the anellus is heavily sclerotized to form a yoke-shaped plate, or juxta (jx), which functions as a support for the aedeagus. The aedeagus (aed) is a long sclerotized tube which enters the ninth somite through the anellus, as stated above. It serves as a protective armature and guide for the penis, or membranous terminal portion of the ejaculatory duct.

The anal armature belongs to the tenth segment, and is composed of two parts. The dorsal process, or uncus (un), is a single, ventrally inclined hook, which projects over the anus. Superficially, the uncus appears to be attached to the tergum, because of the retraction of the tenth segment. The ventral process, or gnathos (gn), consists of paired arms arising from the tergum at the base of the uncus. The median,

ventral plate, which in some insects lies between the arms, is absent and the arms fuse ventrally to form a trough-like projection ventrad of the anus. The anus (an) lies between the uncus and the gnathos. It marks the external opening of the rectum (rec). The rectum is in the form of a membranous tube, and is closely applied to the tergum internally. The membranous area surrounding the anus represents a portion of the tenth abdominal segment.

Female genitalia (Figs. 16, 19)

The eversible female genitalia, which is composed of the highly modified terminal segments of the abdomen, is normally retracted within the seventh somite. It is still further concealed by a thick clothing of long hairs.

The basal portion of the female genitalia is made up of the eighth tergite and sternite. The eighth tergite is a simple semicylindrical plate which narrows abruptly at the point of union with the sternite. A deep invagination is formed at this point, giving rise to an elongated apodeme, or tendon (ten), which extends forward into the body cavity. A similar tendon arises from an invagination in the anterior margin of the ninth segment and extends forward beneath the eighth tergite. Corresponding tendons arise on the opposite side of the genitalia. Muscles involved in the retraction of the genitalia are attached to these tendons.

The ostium (ost), which forms the external opening of the ductus bursae, or vagina, lies ventrad of the eighth tergite. A part of the eighth sternite is modified to form sclerotized lips, or genital plates (gp), surrounding the ostium. Two partially invaginated lobes of the eighth sternite extend cephalad. These lobes are approximated mesally.

Caudad of the eighth segment lies a membranous, tubular extension which functions as an ovipositor. Two sclerotized, hemispherical lobes form the terminus of this extension. These lobes are frequently referred to as the ninth segment, but Snodgrass (1933) states that they evidently represent the united ninth and tenth somites. The lobes are covered with tubercles bearing long setae. The anus (an) and the opening of the vagina, or oviporus (op) of Snodgrass, lie between these lobes. The oviporus is ventrad of the anus. It represents the external opening of the egg duct, and forms a second, or posterior, opening of the genitalia, a condition found only in certain Lepidoptera and in the Mecoptera.

Two short, weakly sclerotized, finger-like processes lie directly below the oviporous. These processes undoubtedly function as auxiliary guides in placing the egg on the host plant.

LITERATURE

Baltzer, A.

1864 Zur Anatomie und Physiologie der Dämmerungsfalter (Sphingidae).
Archiv für Naturgesch. 30: 154-190, pl. IV.

Barnes, W. and McDunnough, J.

1917 A check-list of the Lepidoptera of boreal America: 23-26. Herald Press, Decatur, Illinois.

Braun, Annette F.

1924 The frenulum and its retinaculum in the Lepidoptera.
Ann. Ent. Soc. Amer. 17: 234-256, pl. XVIII.

Burgess, E.

1880 Contributions to the anatomy of the milk-weed butterfly, Danais archippus Fab.
Anniv. Mem. Boston Soc. Nat. Hist. 1-16, pls. I-II.

Busck, August

1931 On the female genitalia of the Microlepidoptera and their importance in the classification and determination of these moths.
Bull. Brook. Ent. Soc. 26: 199-211, pls. IX-XIII.

Busck, A. and Heinrich, C.

1921 On the male genitalia of the Microlepidoptera and their systematic importance.
Proc. Ent. Soc. Wash. 23: 145-152, pls. XII-XIII.

Comstock, J. H.

1918 The wings of insects: 319-346.
Comstock Publishing Co., Ithaca, N. Y.

1930 An introduction to entomology: 29-93; 571-772.
Comstock Publishing Co., Ithaca, N. Y. (Rev. Ed.)

Crampton, G. C.

1917 The nature of the vertex or neck region.
Ann. Ent. Soc. Amer. 10: 187-197, figs. 1-4.

Crampton, G. C. (Cont.)

1919 A phylogenetic study of the mesothoracic terga and wing bases in Hymenoptera, Neuroptera, Mecoptera, Diptera, Trichoptera, and Lepidoptera.
Psyche 26: 58-64, pl. II.

1920 A comparison of the external anatomy of the lower Lepidoptera and Trichoptera from the standpoint of phylogeny.
Psyche 27: 23-34, pls. II-III.

1923 Preliminary note on the terminology applied to the parts of an insect leg.
Can. Ent. 55: 126-132, pl. III.

1926 A comparison of the neck and prothoracic sclerites throughout the orders of insects from the standpoint of phylogeny.
Trans. Amer. Ent. Soc. 52: 199-248, pls. X-XVII.

1928a The eulabium, mentum, submentum, and gular region of insects.
Journ. Ent. and Zool. 20: 1-18, figs. 1-38.

1928b The basal structures of the wings of certain insects.
Bull. Brook. Ent. Soc. 23: 113-116, pl. IV.

1929 The terminal abdominal structures of female insects compared throughout the orders from the standpoint of phylogeny.
Jour. N. Y. Ent. Soc. 37: 453-496, pls. IX-XVI.

1931 A phylogenetic study of the posterior metathoracic and basal abdominal structures of insects, with particular reference to the Holometabola.
Jour. N. Y. Ent. Soc. 39: 323-357, pls. XX-XXIV.

1932 A phylogenetic study of the head capsule in certain Orthopteroid, Psocid, Hemipteroid, and holometabolous insects.
Bull. Brook. Ent. Soc. 27: 19-50, pls. IV-VIII.

Dyer, J. R.

1924 The comparative morphology of the male genitalia of the primitive Lepidoptera.
Ann. Ent. Soc. Amer. 17: 275-328, pls. XXV-XXXVIII.

Fernald, C. H.

1886 The Sphingidae of New England: 85 pp., pls. I-VI.
Sprague and Sons, Agusta, Maine.

Forbes, W. T. M.

1923 The Lepidoptera of New York and neighboring states. Cornell Univ. Ag. Ex. Sta. Memoir 68: 1-729.

Holway, R. T.

1933 The external morphology of the clouded sulphur, Colias philodice Godart. Unpublished thesis, Mass. State College; 46 pp.

1937 The comparative morphology of the insect pretarsus. Unpublished thesis, Mass. State College; 101 pp.

Imms, A. D.

1930 A general textbook of entomology; 698 pp. Methuen and Co., London.

Kellogg, V. L.

1895 The mouth parts of Lepidoptera. Amer. Naturalist 29: 546-556, 1 pl.

Martin, J. F.

1916 The thoracic and cervical sclerites of insects. Ann. Ent. Soc. Amer. 9: 35-83, pls. I-IV.

Mosher, E.

1915 Homology of the mouthparts of the pre-imago in Lepidoptera. Jour. Ent. and Zool. 7: 98-106, figs. 1-23.

1918 Pupae of common Sphingidae of eastern North America. Ann. Ent. Soc. Amer. 11: 403-441, pl. XXXVI.

McDunnough, J.

1911 On the nomenclature of the male genitalia in Lepidoptera. Can. Ent. 43: 181-189.

1938 Check list of the Lepidoptera of Canada and the United States of America. Part I. Macrolepidoptera. Mem. So. Calif. Acad. Sci. 1: 36-41.

Peterson, A.

1912 Anatomy of the tomato-worm larva, Protoparce carolina. Ann. Ent. Soc. Amer. 5: 246-269, pls. XIX-XXI.

Peterson, A. (Cont.)

1916 The head-capsule and mouth-parts of Diptera.
Ill. Biol. Mon. 3: 1-62, pls. I-XXV.

Rothschild, W. and Jordan, K.

1903 Revision of the Sphingidae.
Nov. Zool. 9: 1107 pp., 67 pls. (suppl.)

Schmitt, John B.

1938 The feeding mechanism of adult Lepidoptera.
Smiths. Misc. Coll. 93 (4): 28 pp., 12 figs.

Schultz, H.

1914 Das Pronotum und die Patagia der Lepidoptera.
Deutschen Entomolog. Zeitschr. Part I: 17-42,
9 pls.

Shepard, H. H.

1930 The pleural and sternal sclerites of the lepidopterous thorax.
Ann. Ent. Soc. Amer. 23: 237-254.

Smith, John B.

1888 A monograph of the Sphingidae of America north of Mexico.
Trans. Amer. Ent. Soc. 15: 49-242, pls. IV-XIII.

Smith, M. E.

1936 A contribution to the morphology and the distribution of the Arctiidae of New England.
Unpublished thesis, Mass. State College; 95 pp.

Snodgrass, R. E.

1909 The thorax of insects and the articulation of the wings.
Proc. U. S. Nat. Mus. 36: 511-595, pls. 40-69.

1928 The morphology and evolution of the insect head and its appendages.
Smiths. Misc. Coll. 81 (3): 158 pp., 57 figs.

1931 Morphology of the insect abdomen. Part I. The general structure of the abdomen and its appendages.
Smiths. Misc. Coll. 84 (6): 128 pp. 46 figs.

Snodgrass, R. E. (Cont.)

1932 Evolution of the insect head and the organs of feeding.
Smiths. Ann. Report 1931: 443-489, 25 figs.

1933 Morphology of the insect abdomen. Part II. The genital ducts and the ovipositor.
Smiths. Misc. Coll. 89 (8): 148 pp., 48 figs.

1935 Principles of insect morphology; 667 pp.
McGraw Hill Co., New York.

1936 Morphology of the insect abdomen. Part III. The male genitalia.
Smiths. Misc. Coll. 95 (14): 96 pp., 29 figs.

Weber, Hermann

1928 Die Gliederung der Sternopleuralregion des Lepidopterenthorax.
Zeitschrift für wissenscheftliche Zoologie. 131: 181-254, 21 figs.

ABBREVIATIONS

A - anal vein
a - anepisternal suture
acs - antecostal suture
ad - adanale
aed - aedeagus
aes - anepisternum
al - adnotale
an - anus
anf - antennifer
ant - antenna
ar - arolium
as - antennal suture
asc - antennal sclerite
at - anterior arm of tentorium
atg - acrotergite
au - anellus
ax - axillary
axc - axillary cord

ba - basalare
bc - basicostal suture
bp - basalar pad
bpl - basoplica
bs - basisternum
bt - basitarsus

C - costa
cd - cardo
cg - cephaliger
cil - cilia
Cu - cubitus
cx - coxa

dc - discal cell
dlcb - dilator muscle of cibarium
dlphy - dilator muscle of pharnyx
dt - distitarsus

e - compound eye
ecx - eucoxa
em - epimeron
emp - empodium

ep - epipharnyx
epi - epiphysis
eps - episternum

f - frenulum
fa - furcal arm
fc - fronto-clypeus
fe - femur
fl - flagellum
fp - frontal pit
fr - frontal suture
fs - furcasternum

ga - galea
gn - gnathos
gp - genital plate

hbr - hypostomal bridge
hp - humeral plate
hr - harpe
hy - hypopharnyx

jx - juxta

kes - katepisternum

lc - lateral cervical sclerite
lm - labrum
lp - labial palpus

M - media
m - proximal median plate
m' - distal median plate
m-cu - medio-cubital cross-vein
md - mandible
me - meron
mp - maxillary palpus
mv - mid-ventral suture

ni - notal incision

oc - ocular sclerite
ocd - occipital condyle
ocf - occipital foramen
ocp - occiput
oes - oesophagus
op - oviporus
or - orbicula
os - ocular suture
ost - ostium

p - pedicel
pa - pleural arm
pad - postadanale
par - parapatagium
pem - prepimeron
pes - prepisternum
pfr - pilifer
pg - Patagium
pge - postgena
pgs - postgenal suture
ph - postphragma
pl - planta
pm - presternum
pr - pronotum
poc - postoccipital sclerite
por - postoccipital ridge
pos - postoccipital suture
pr - precoxale
pra - prealar
ps - pleural suture
psc - prescutum
pscl - postscutellum
pt - posterior arms of tentorium
pu - pleural sclerite
pv - pulvillus

R - radius
r - marsupium
rs - radial sector
rec - rectum

s - sternite
sa - subalare
sac - sacculus
Sc - subcosta
sc - head of subcosta
scl - scutellum
scn - sense cone

scp - scape
sct - scutum
sd - salivary duct
sgs - subgenal suture
so - scent organ
sp - spiracle
sps - sucking pump
spu - spur
ss - spinasternum
st - subtegula
stp - stipes
sw - saccus
sur - surstylus

t - tergite
tb - tibia
teg - tegula
ten - tendon
tg - tergum
ti - tegular incision
tp - tergo-pleural groove
tr - trochanter
trn - trochantin
ts - transtilla

u - precoxisternal suture
un - unguis
ung - unguis
ut - unguitractor
utt - unguitractor tendon

v - vinculum
vx - vertex

wp - pleural wing process

x - epicoxal piece

EXPLANATION OF FIGURES

Fig. 1. Frontal view of the head (left antenna and palpus removed)
Fig. 2. Antenna of female
Fig. 3. Lateral view of a segment of the male antenna
Fig. 4. Caudal view of the head (right palpus removed)
Fig. 5. Antenna of male
Fig. 6. Internal view of left half of the head
Fig. 7. Prothoracic leg

Fig. 8. Dorsal view of thorax (right tegula removed)
Fig. 9. Fore-wing
Fig. 10. Hind wing
Fig. 11. Mesothoracic leg
Fig. 12. Metathoracic leg
Fig. 13. Lateral view of thorax (tegula removed)

Fig. 14. Lateral view of abdomen of the male
Fig. 15. Pretarsus
Fig. 16. Lateral view of female genitalia
Fig. 17. Lateral view of male genitalia
Fig. 18. Ventral view of pro- and mesothoraces
Fig. 19. Ventral view of female genitalia

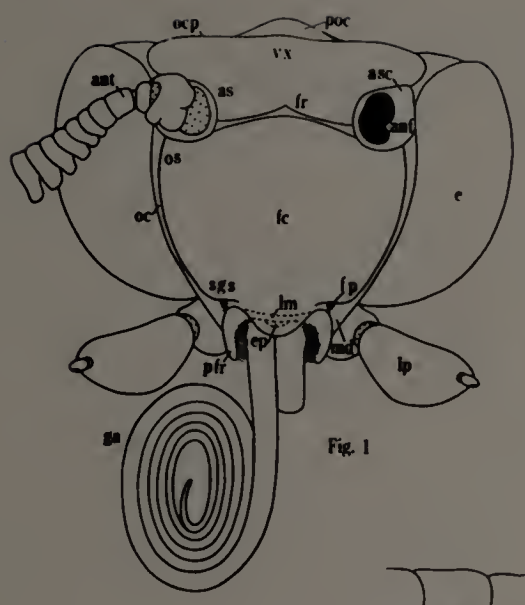

Fig. 1

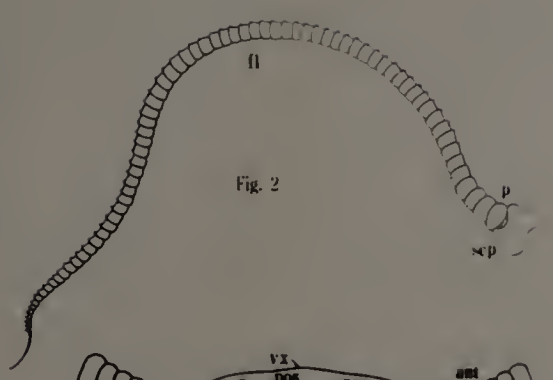

Fig. 2

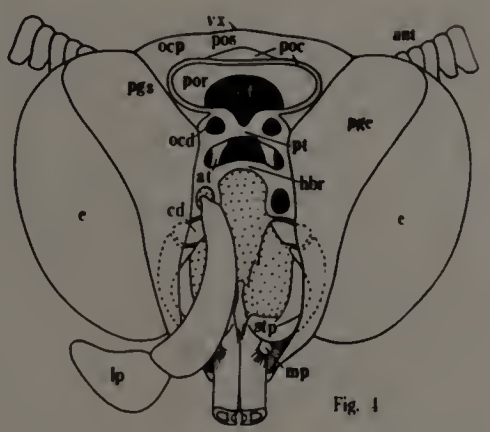

Fig. 4

Fig. 3

Fig. 5

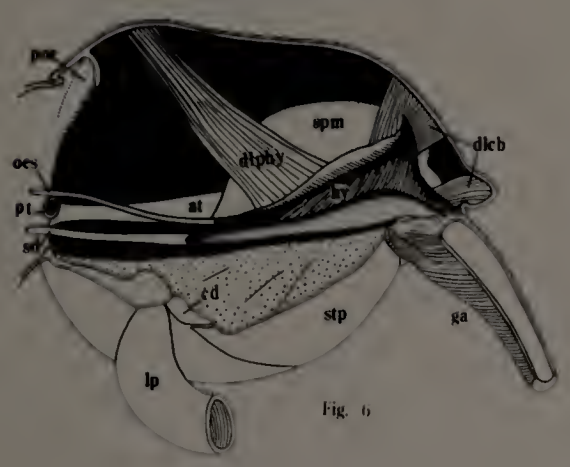

Fig. 6

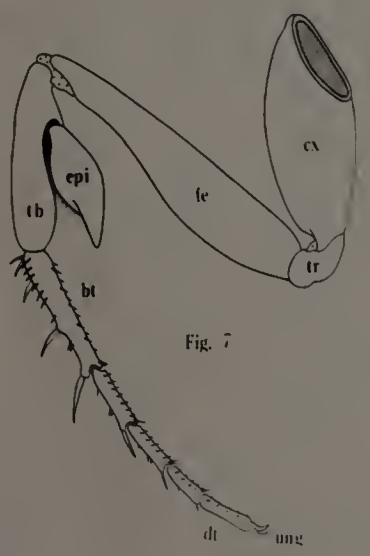

Fig. 7

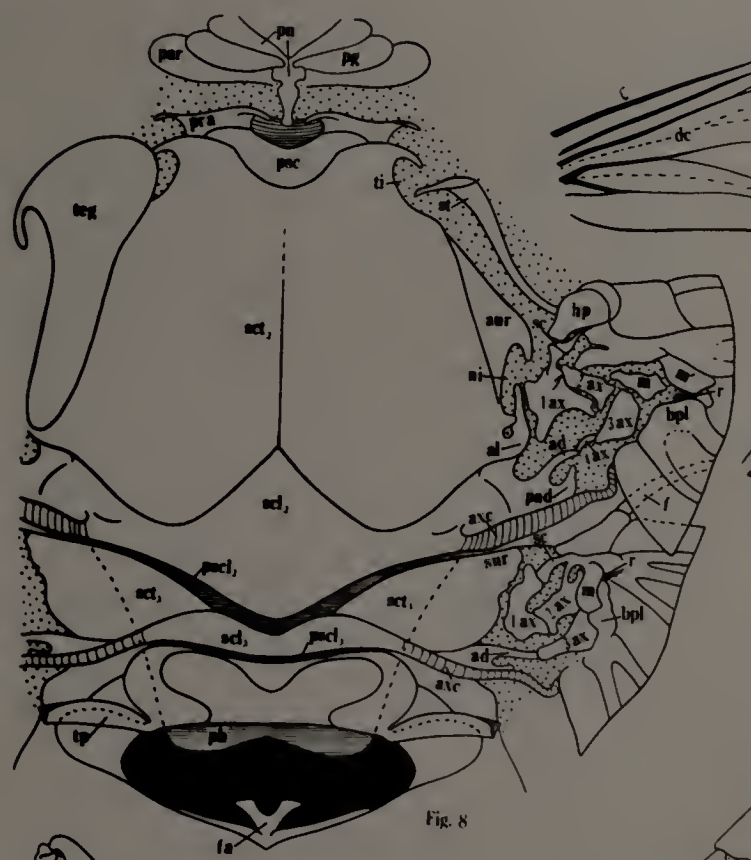

Fig. 8

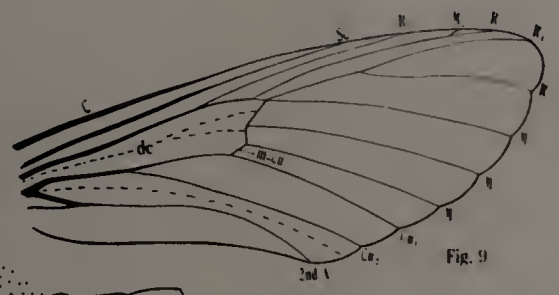

Fig. 9

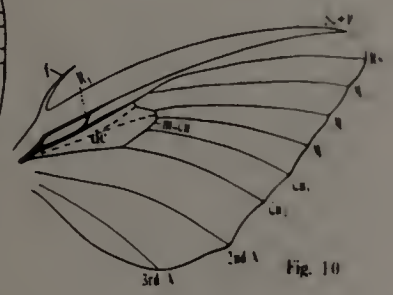

Fig. 10

Fig. 11

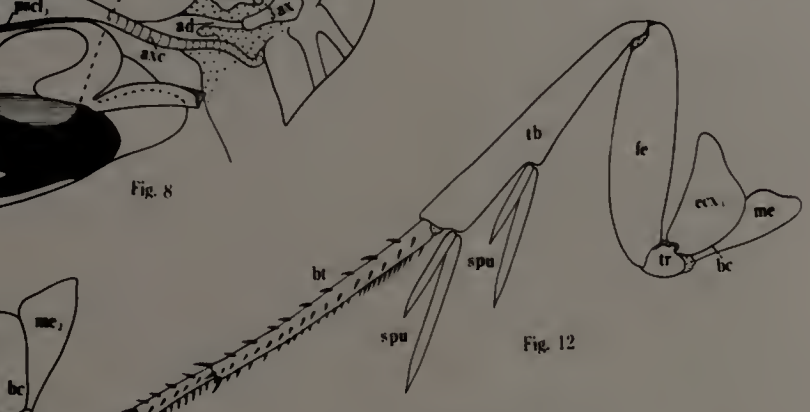

Fig. 12

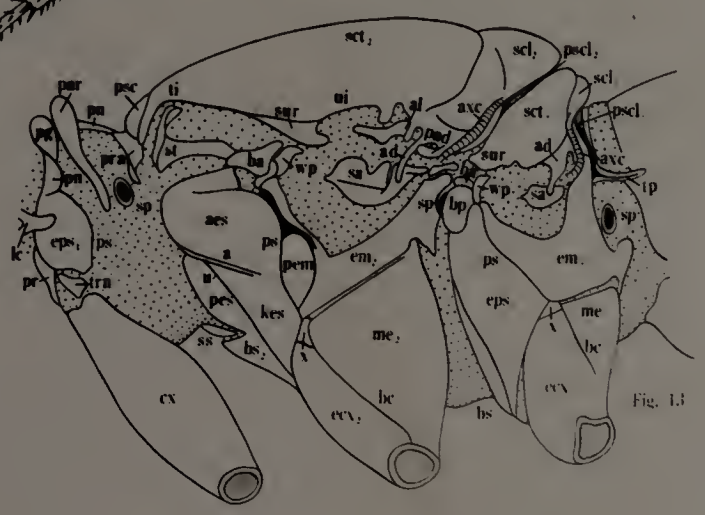

Fig. 13

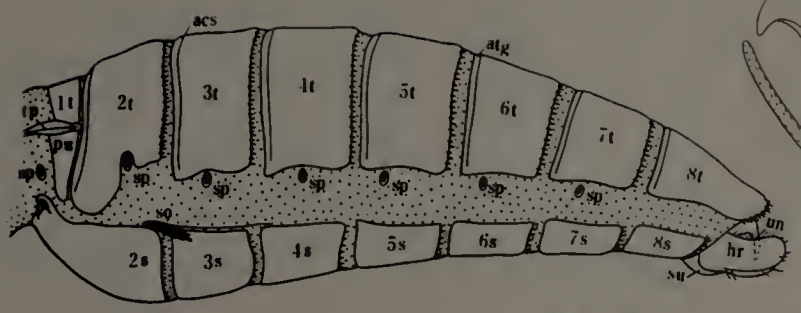

Fig. 11

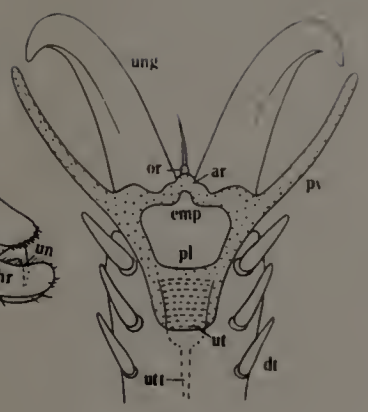

Fig. 15

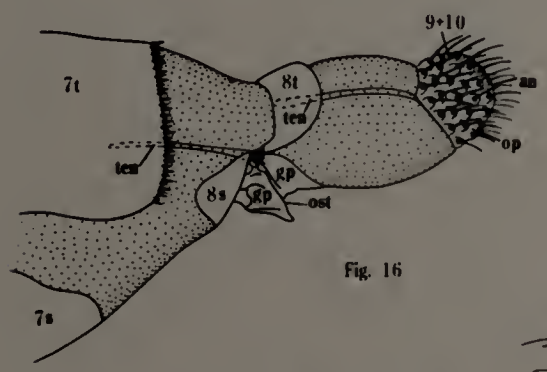

Fig. 16

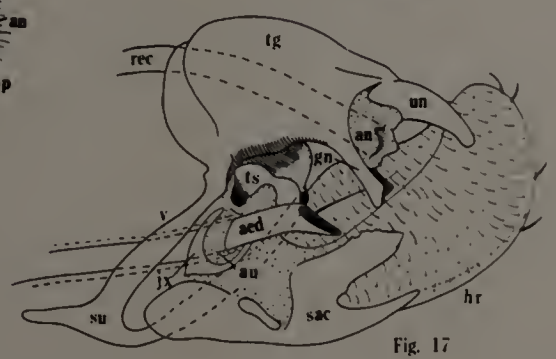

Fig. 17

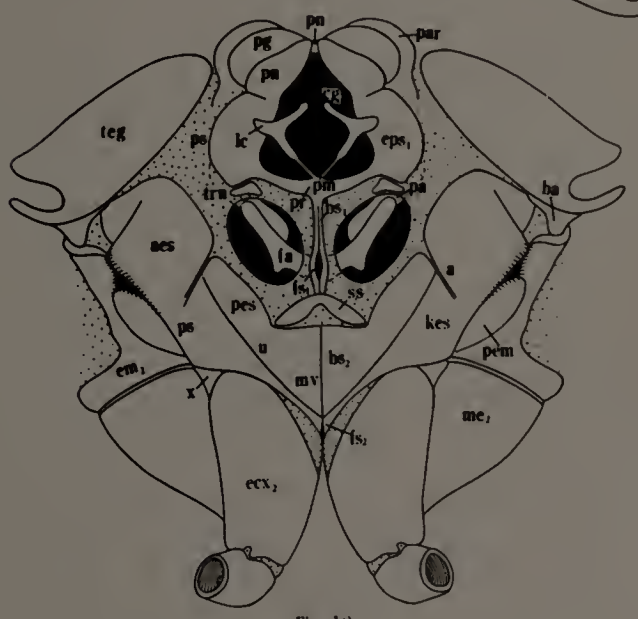

Fig. 18

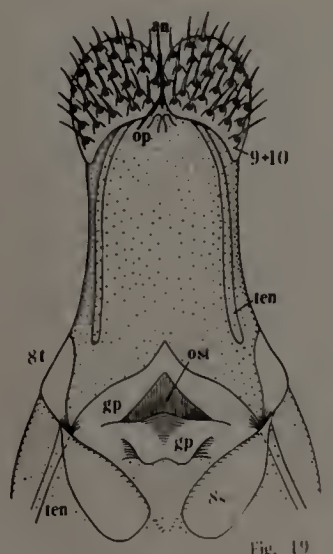

Fig. 19

Approved by:

Charles P. Alexander

H. A. Davis

E. V. Wilcox

Graduate Committee

Date May 2, 1939.